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CENTRAL REPRESENTATION OF AFFECTIVE REACTIONS IN FOREBRAIN AND BRAIN STEM: ELECTRICAL STIMULATION OF AMYGDALA, STRIA TERMINALIS, AND ADJACENT STRUCTURES

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Ever since Bard (1928) demonstrated on cats that rage reactions readily develop after decortication and transection of the brain stem at the level of the diencephalon, the attention of workers has been directed toward the role played by the diencephalon and mesencephalon in the government of these reactions. Ranson & Magoun (1933) by electrical stimulation of the hypothalamus in cats with the head fixed in a stereotaxic apparatus obtained spitting; Magoun, Atlas, Ingersoll & Ranson (1937) from the central gray matter of the mid-brain and the adjacent tegmentum produced hissing and crying. On the waking, freely moving cat, Hess & Brügger (1943) elicited an affective defence reaction, i.e. hissing, lowering of the head, flattening of the ears, marked dilatation of the pupils, and pilo-erection on back and tail, by stimulation of the 'perifornical' region of the hypothalamus. Flight responses have also been produced by stimulation of the posterior hypothalamus and the adjacent subthalamic region (Hess, 1949, 1957). Hunsperger (1956) obtained the affective defence reaction, not only from the 'perifornical' region of the hypothalamus, but also from the central gray matter of the mid-brain, these two areas being surrounded by a larger common field from which flight responses were obtained. It was therefore concluded that the substratum concerned with these various patterns of emotional behaviour constitutes an unbroken field, comprising portions of the central gray matter of the preoptic area, the hypothalamus and the mid-brain. The reactions were strikingly similar to those seen when a cat is confronted by a dog, but did not appear to be the pain-suggestive reactions reported by Spiegel, Kletzkin & Szekely (1954) in the unrestrained cat, and by Delgado (1955) in the monkey.

Affective responses, besides motor and autonomic effects, have also been produced by electrical stimulation of the amygdala and adjacent structures in the forebrain (secondary forebrain, telencephalon) in unrestrained cats. Thus MacLean & Delgado (1953) reported growling and hissing, organized angry behaviour, as well as efforts to escape; Magnus & Lammers (1956), growling and anxious behaviour. Gastaut, Naquet, Vigouroux & Corriol (1952), Naquet (1953), Kaada, Anderson & Jansen (1954), and Kaada & Ursin (1957) obtained with weak stimulation an attention response accompanied by contraversive turning of the head or searching movements to the opposite side; stronger stimulation yielded fear and anger reactions that were characterized by maximal dilatation of the pupils, pilo-erection, lowering of the head, flattening of the ears, and either flight, or growling, hissing, gnashing of the teeth, clawing and arching of the back, accompanied by accentuated turning movements also involving the trunk. Shealy & Peele (1957) obtained similar affective reactions, and associated the facial motor effects, sniffing, salivation, and movements of the tongue, obtained simultaneously, with the responses. All these authors agree that the responsive area is predominantly located in the medially lying portions of the amygdala, although Kaada and his collaborators (Kaada *et al.* 1954, 1957) extend the field to the lateral, and Magnus & Lammers (1956) to ventral portions of the amygdala, MacLean & Delgado (1953) to the adjacent pyriform cortex and hippocampus, and Kaada, Jansen & Anderson (1953) to the hippocampus and fimbria fornicis.

All these investigations show that affective reactions have their central representation in the brain stem as well as in the forebrain. That the amygdala in the forebrain, and septum and hypothalamus in the brain stem are linked together by a common path, the stria terminalis, has been established by many anatomical studies (Johnston, 1923; Fox, 1940, 1943; Ariëns Kappers, Huber & Crosby, 1936; Droogleever Fortuyn, 1956) and, recently, by electrophysiological experiments (Gloor, 1955). Whether the stria terminalis, however, is concerned with emotional responses, and whether a distinction can be made, or not, between the effects obtained from the forebrain and the brain stem, still remained to be investigated. It was therefore decided to explore, not only the amygdala and the adjacent hippocampus, but also the paths that connect these structures with the septal area and the hypothalamus, paying particular attention to the following points:

1. Exact pattern of the reactions elicited from the amygdala and related structures in the forebrain;
2. Comparison of these reactions with the effects obtained in previous experiments from the hypothalamus and mid-brain;
3. Delimitation of the anatomical structures concerned;
4. Whether forebrain and brain-stem fields are linked functionally, and so constitute an entity.

In order to ensure conformity in the methods used, and to facilitate comparison, the Hess–Wyss technique of previous experiments was employed. A preliminary report of this study has recently been published (Fernandez de Molina & Hunsperger, 1957).

METHODS

Forty-seven adult cats of both sexes were used, body weight 2–4·5 kg. The procedure described by Hess (1932, 1957) was applied in order to study the responses to brain stimulation of the unanaesthetized freely moving animal. Stimulating electrodes consisted of single needles, each 0·3 mm in diameter, with tip bared for 1 mm. Three needles were arranged in a sagittal line, 1·5 mm distant from one another. They were inserted 8, 4, or 2·5 mm from the mid line, so that by lateral or medial inclination their tips could be placed between 12 and 1 mm from mid plane. The three needles were inserted with the middle needle through the coronal suture or up to 11·5 mm more caudally. The needles measured between 18 and 28 mm from skull surface to tip.

Exploration was usually restricted to one brain structure, examined bilaterally. In eight animals, however, other structures were examined in a second stage of the experiment for the sake of comparison. In four cats 10 days intervened between first and second exploration. A total of 405 'points', i.e. electrode positions, were explored; of these 240 were located in the amygdala, the remaining 165 were in structures connecting the amygdala and the adjacent hippocampus with the brain stem.

Unipolar stimulation was used, the indifferent electrode, connected to the metal frame screwed on the skull, being earthed. Delayed condenser discharges delivered by a Wyss (1950) type stimulator, with a rising phase of 10 msec maintained constant throughout, were applied through a 30 μF condenser and a 10 kΩ resistor to the needle electrode serving as cathode. The voltage of the stimulating electrode as referred to earth and the current flowing through it were amplified and displayed with common sweep triggered by stimulation frequency on a double-beam cathode-ray tube (Cossor). An ordinate-calibrated photograph was taken during each stimulation period.

Each area explored was initially stimulated with a frequency of 8·5 c/s and a voltage ranging from 0·75 to 3 V, and then with a frequency of 17 c/s and a voltage up to 2 V. Higher rates (28 c/s) did not give any noticeable change in the response already evoked with lower frequencies. Each stimulation period lasted 1 min. An interval of 1–3 min or more was allowed between successive stimulations.

Responses observed were recorded by protocol and film. The brains were serially sectioned in a frontal plane and alternate sections (celloidin, 40 μ) were stained by Nissl and Heidenhain techniques. The electrode locations were examined histologically, the end of each needle track being plotted on a series of photographs of standard brain sections (Hess, 1932). The 'points' were grouped according to the responses obtained and each group marked on a second series of photographs.

RESULTS

The area from which the affective reactions described in this paper were elicited occupies the dorsomedial region of the amygdala. It can be traced along the pathway of the stria terminalis into the bed nucleus of this tract at the level of the anterior commissure. At this level the responsive points lie spread out and join the active field in the preoptic area and the rostral hypothalamus described in previous papers (Hess & Brügger, 1943; Hunsperger, 1956). The responses from this zone included: growling, growling followed by hissing or by shrieking, and growling-hissing leading to flight; primary hissing and primary flight.

Pattern of responses

The growling response developed as follows: The animal before onset of stimulation sat or lay quietly on the table. Soon after stimulation set in, the cat turned its head toward the observer, the lids widened, the pupils dilated and respiration increased in depth and rate. The eyes remained fixed on the observer and the animal appeared to be taut. A first low growl was then emitted, chin protruded and upper lip pursed, followed by louder growls uttered at intervals of 5–10 sec. Often the pupils dilated maximally, the ears were laid back, the head was lowered and pilo-erection of back and tail set in (Plate 1*b*). The growling sometimes alternated with short puffing expirations during which the animal stood up and slightly hunched its back.

When the response evoked was *growling followed by hissing*, the growls toward the end of stimulation were replaced by raucous, repeated hissing; the mouth was opened wide, with corners retracted, teeth bared (Plate 1*c*). Although the cat turned its head toward the observer, the animal never attacked. In this group the general defence pattern, i.e. dilatation of the pupils, flattening of the ears, lowering of the head, pilo-erection, and slight hunching of the back, was more marked than in the growling group. When stimulation produced *growling followed by shrieking*, the growls, low at first, gradually became louder and gave way to strident shrieks. When the growling-hissing response led to *flight*, the animal toward the end of stimulation excitedly turned eyes and head to either side, but instead of growling or hissing sidled across the table with a frightened expression. A sudden leap, clearing all obstacles, landed the animal on the floor.

The *primary hissing response* was accompanied by the general defence pattern already described. The *primary flight response* developed in the following manner. The pupils, after onset of stimulation, dilated, the eyes darted to and fro, the head turned, occasionally pilo-erection set in, and suddenly the cat rushed off the table.

After cessation of stimulation excitement subsided gradually and the animal settled down, apparently relaxed. In a few cases, however, the cat remained for a few seconds or even minutes in the posture assumed when stimulation ceased. It looked puzzled, with pupils remaining dilated, and was indifferent to slight visual stimuli or hand clapping. Plaintive or protesting mewing sometimes terminated this state. Flight was rarely observed after switching off stimulation.

The stimulation threshold was lowest for the growling response. In 13 of the 63 cases in which growling was obtained, the response developed even with the low stimulation frequency of 8·5 c/s and a voltage not exceeding 1·5 V. These 13 points lay widely dispersed within the active field, the lowest threshold of 1·0 V being obtained from one of the six needles placed in the track of the stria terminalis alongside the lateral ventricle. It was only by increasing strength or rate of stimulation that growling gave way to hissing, shrieking or flight. The hissing had an average threshold that was 1·5 times higher than the threshold for growling at the stimulation frequency of 8·5 c/s, and 1·25 times higher at the frequency of 17 c/s. The primary hissing response and the hissing which replaced growling had approximately the same threshold. The average thresholds for the primary flight response and the growling response were equivalent.

Latency ranges for growling were from 3 to 60 sec, for hissing replacing growling from 7 to 60 sec, for the primary flight response from 7 to 20 sec. The latency depended on the site of stimulation and on the stimulation strength and rate. The mean latency for growling was decreased to half when intensity was increased either 50 % above threshold at the frequency of 8·5 c/s, or 20 % above threshold at the frequency of 17 c/s. The latency for hissing replacing growling was on an average twice as long as that for growling, this including both frequencies.

Distribution of the responsive points within the active area

The affective reactions described above were evoked by stimulation of a total of 73 points. Growling was obtained from 63; of these, 28 yielded growling followed by hissing, 5 growling followed by shrieking and 4 growling-hissing leading to flight. The stimulation of 3 points produced the primary hissing response, the stimulation of 7 points the primary flight response.

Identical growling and growling-hissing responses were obtained from the amygdala, the track of the stria terminalis, and the stria terminalis bed. The growling-hissing response was, however, obtained relatively more often from the stria terminalis bed than from the amygdala. The points yielding the primary hissing response lay in the stria terminalis bed and in the preoptic area. Growling followed by shrieking was obtained from the amygdala and the track of the stria terminalis, but not from the stria terminalis bed. Growling-hissing leading to flight was produced from the amygdala as well as from the stria terminalis bed, and so was the primary flight response. The points in the amygdala yielding the primary flight response were not grouped, but lay scattered between those yielding growling and growling-hissing (see Text-fig. 1*B*).

Two other active points (not dealt with in this study) were situated in the preoptic area and the anterior hypothalamus and yielded reactions described in a previous report (Hunsperger, 1956).

Factors affecting the type of the response

Repeated stimulation of one point may change the type of the response. In four cases growling was obtained as a low-threshold response; successively stronger stimuli failed to produce the reaction, but still stronger stimuli elicited a pure flight response. In two other cases, however, this final response was not obtained.

The primary flight response appeared to be more readily evoked when previous stimulation from some other point produced an affective discharge.

When the primary flight response was obtained at a low threshold, increased stimulation again produced flight; attempts to hinder escape, however, provoked growling or hissing in most cases.

The individual character of the cat (as far as could be judged in the laboratory) may affect the reactions. It was noted that the flight response was more easily elicited in timorous and suspicious animals than in those that appeared to be at their ease in the laboratory.

Other effects elicited within the active area

In half of all the cases yielding affective reactions, effects were obtained which are not necessarily related to emotional behaviour. Thus micturition frequently, and defaecation less frequently, occurred simultaneously with affective reactions; the animal never assumed an adequate posture. The affective reactions were preceded by one or several of the following effects; sniffing, facial motor effects (rhythmic twitching of the eyelid and vibrissae, generally ipsilateral), salivation and movements of the tongue as if to eject a foreign body (Hess & Akert, 1951) and retching. During the emotional response itself these effects were suppressed, but twitching of the eyelid and vibrissae, movements of the tongue and profuse salivation often reappeared when stimulation ceased. In other cases growling-hissing were preceded *and* accompanied by a contralateral turning of eyes and head, or a repeated jerking of eyes and head to the side opposite the stimulation; these supplementary effects often outlasted the stimulation. In one case growling was accompanied by a generalized epileptic seizure.

It should be noted that all these supplementary effects were obtained from points scattered throughout the active area. They could also be elicited as extraneous effects from points situated beyond the limits of the active field.

Topography of the active area and location of extraneous effects

The active points, which are indicated on Text-fig. 1 by black and white circles and squares, within the amygdala, are located in the dorsal portion of the nucleus basalis and adjacent parts of the nucleus centralis and nucleus medialis, i.e. in a field from which several components of the stria terminalis arise (Text-fig. 1*B*). From this area the site of the active points can be traced beyond the amygdala and is strictly limited to the narrow track followed by the stria terminalis on its way to the bed nucleus at the level of the anterior commissure (Text-fig. 1*B–G*). Active points are distributed throughout the bed nucleus, and are traceable from here into preoptic area and rostral hypothalamus (Text-fig. 1*H*).

Stimulation of a total of 332 points located outside the active area, using the same voltages and rates as those which yielded affective reactions, failed to produce an emotional response. The location of points yielding these extraneous effects is indicated in Text-fig. 1 by dots. The big circles mark out a grouping of points yielding one effect, or several, indicated by the symbols placed adjacent to the circles. The location of these points was as follows:

(a) *Structures in close topographical relation to the active area.* Within the amygdala, i.e. medial and caudal portions of the nucleus lateralis, ventral part of the nucleus basalis and nucleus medialis, lateral part of the nucleus centralis, nucleus corticalis, anterior amygdaloid area and adjacent portions of pyriform cortex. Stimulation of these structures produced one or several of the effects mentioned in the preceding section, p. 256, but unaccompanied by affective reactions (Text-fig. 1*A–C*). It should be noted that the commissural component of the stria terminalis (component 1 of Johnston, 1923) stimulated within the amygdala, never yielded affective reactions. Stimulation of the longitudinal association bundle (Fox, 1940), within the amygdala and beneath the pallidum, lateral to the hypothalamus, also proved negative (Text-Fig. 1*B*, *A*).

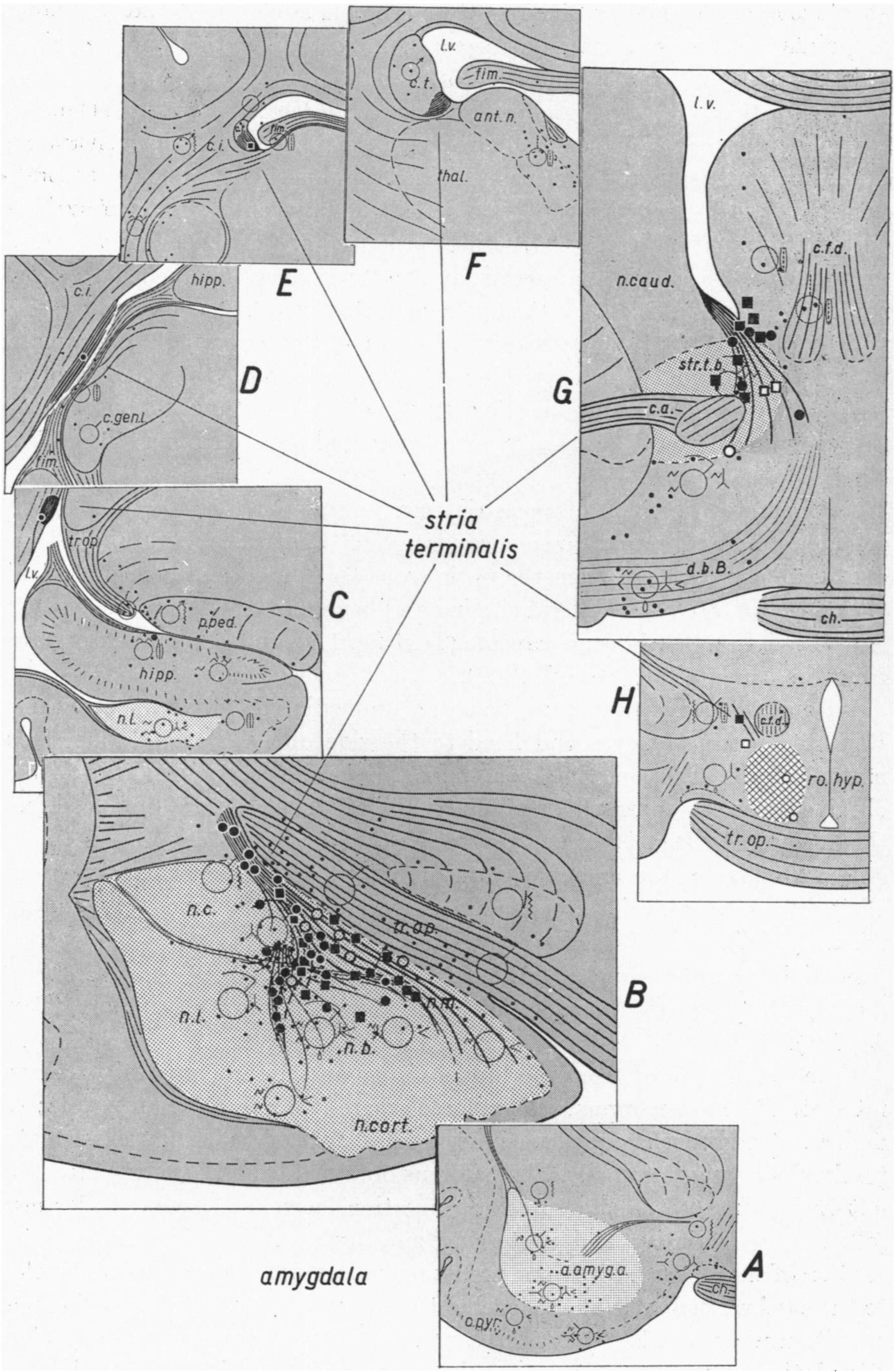
Adjacent to the track of the stria terminalis, i.e. optic tract and lateral geniculate body, internal capsule, caudate tail. Contralateral turning of eyes and head was obtained from the optic tract and the lateral geniculate body (Text-fig. 2*B–D*), contralateral circling and generalized tremor of the contralateral side from the internal capsule (Text-fig. 1*E*), and contralateral circling from the caudate tail (Text-fig. 1*F*).

Within the stria terminalis bed and immediately adjacent structures. Repeated jerking of eyes and head to the side opposite stimulation, facial motor effects and sometimes sniffing—the effects being similar to those obtained from the extraneous points in the amygdala—were produced from this region (Text-fig. 1*G*).

Bed nucleus of the diagonal band of Broca: Effects identical with those elicited from the anterior amygdaloid area were obtained from this structure (Text-fig. 1*G*).

Medial forebrain bundle (stimulated within the lateral preoptic area): Sniffing and sometimes salivation were evoked from this bundle (Text-fig. 1*H*).

Responses obtained from the hippocampus and fimbria were of particular interest. The hippocampus was explored where it borders the amygdala; the fimbria at various levels, using nine needles, five of which lay close to the track of the stria terminalis. The patterns obtained from the active area were not evoked from these structures. Stimulation, however, produced alertness, followed by plaintive and protesting mewing several seconds after interruption of the current. Only one point within the hippocampus, situated close to the cerebral peduncle at the level of the corpus Luys, yielded growling and, simultaneously, marked generalized tremor of the contralateral side. When stimulation was stronger than usual (frequency 17 c/s, 2–3 V) growling was



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added to the effects obtained from four of the eight points situated in the area of transition amygdala-hippocampus.

(*b*) *Structures anatomically related to the active area in the hypothalamus.* The descending column of the fornix (stimulated at the level of the anterior

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Legend to Text-figure 1.

Text-fig. 1. Semi-schematic illustration showing location of points yielding affective reactions in amygdala, stria terminalis, stria terminalis bed and rostral hypothalamus. Frontal sections. Points lying up to 0·75 mm rostral or caudal to the plane shown are also included in these diagrams. *A*, through anterior amygdaloid area (×3·5); *B*, through middle portion of the amygdala (×7); *C*, through hippocampus close to amygdala (×3·5); *D*, through stria terminalis and fimbria (×3·5); *E*, the same at more rostral level (×3·5); *F*, the same at level of anterior nuclei of thalamus (×3·5); *G*, through stria terminalis bed (×5·5); *H*, through rostral hypothalamus (×4·5): planes of section (see also Text-fig. 2).

● growling response;

■ growling followed by hissing or shrieking, and growling-hissing leading to flight;

□ primary hissing response;

○ primary flight response;

active field in rostral hypothalamus;

• negative points with regard to affective reactions; yielding, however, the effects indicated by symbols in their vicinity;

◯ represent the fields from which one or several effects were obtained;

/ contralateral, \ ipsilateral turning of eyes and head;

repeated jerking of eyes and head to the side opposite stimulation;

↗ contralateral circling;

rhythmic twitching of eyelid or of vibrissae;

∧∧ pricking of the ears;

general tremor of the contralateral side;

sniffing;

salivation;

< movements of the tongue as if to eject a foreign body;

—< retching;

! mewing during stimulation;

(!) mewing following cessation of stimulation.

amyg. amygdala; *a.amyg.a.* anterior amygdaloid area; *ant.n.* anterior nuclei of the thalamus; *c.pyr.* pyriform cortex; *c.i.* internal capsule; *c.t.* caudate tail; *ch.* chiasma; *c.f.d.* descending column of the fornix; *c.a.* anterior commissure; *c.gen.l.* lateral geniculate body; *d.b.B.* diagonal band of Broca; *fim.* fimbria; *gr.c.mes.* central gray matter of the mesencephalon; *hipp.* hippocampus; *hyp.* hypothalamus; *l.v.* lateral ventricle; *n.b.* nucleus basalis of the amygdala; *n.caud.* caudate nucleus; *n.c.* central nucleus of the amygdala; *n.cort.* cortical nucleus of the amygdala; *n.l.* lateral nucleus of the amygdala; *n.m.* medial nucleus of the amygdala; *p.ped.* cerebral peduncle; *ro.hyp.* rostral hypothalamus; *str.t.* stria terminalis; *str.t.b.* stria terminalis bed; *thal.* thalamus; *tr.op.* optic tract.

commissure), mammillary bodies and their projection field in the thalamus, i.e. anterior nuclei. Alertness was produced from the fornix and the anterior nuclei of the thalamus, accompanied by mewing that outlasted stimulation (Text-fig. 1*F*, *G*). The animal manifested increased interest in its surroundings when the mammillary bodies were stimulated. Extraneous points were also situated beneath the pallidum in an area that lies between the anterior amygdaloid region and the rostral hypothalamus (Text-fig. 1*A*, *H*).

DISCUSSION

Response patterns

The results reported in this paper show that growling and growling-hissing are integrated in a general defence pattern and that these responses are in most instances obtained without accompanying contraversive turning of eyes and head or repeated jerking of eyes and head to the side opposite stimulation reactions recalling the responses described by Gastaut *et al.* (1952) as 'mouvement de contraversion' and by Kaada *et al.* (1953, 1954, 1957) as 'attention and searching responses'. The absence of these motor components and the fact that they are obtained also as extraneous effects from structures outside the active area of amygdala and stria terminalis bed strongly suggest that these motor components do not form an integrative part of the basic growling-hissing responses. The same holds true for the facial motor effects, salivation, movements of the tongue and retching, effects that sometimes preceded the basic reactions and were regarded by Shealy & Peele (1957) as being related to rage responses.

The present results, growling and hissing integrated in a defence pattern, are not in agreement with the effects reported by MacLean & Delgado (1953): growling and hissing obtained as isolated components of angry states by stimulation of the amygdala. These authors report organized angry behaviour from the 'rostral' hippocampus and the region where amygdala, hippocampus and pyriform cortex converge, effects occasionally obtained in our series from the area of transition amygdala-hippocampus, and then only with stronger stimulation than usual.

Stimulation of the amygdala in man by implanted electrodes is reported by Heath, Monroe & Mockley (1955) to lead to a subjective experience of rage; subsequent stimulation with the same intensity produced intense fear with an impulse to run. There is reason to believe that these subjective reactions in man are comparable with the integrated 'acting out' manifestations in the cat. The change in character of the subjective feeling in man, and the change in character of the response occasionally produced by repeated, increased stimulation in the cat, also seem to be analogous and based on a similar mechanism.

Topographical aspects

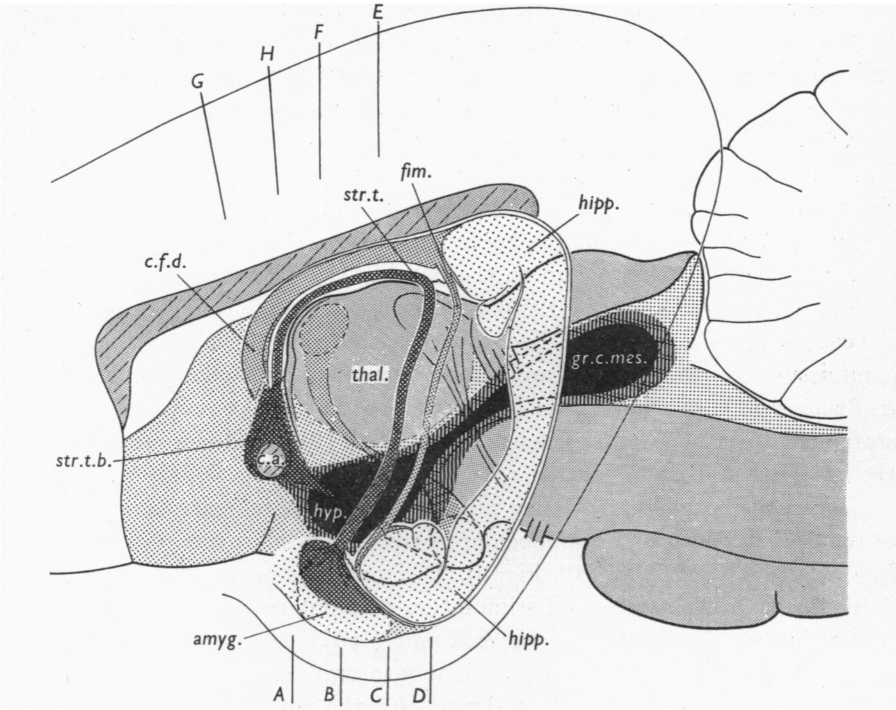
The site of active points reveals a striking overlapping with the fine and numerous fibres of the stria terminalis (components 2, 3? and 4 of Johnston, 1923) that arise in dorsomedial portions of the amygdala and project to the stria terminalis bed and in part to the 'perifornical' region of the hypothalamus (Fox, 1940, 1943; Verena M. Bucher & R. W. Hunsperger, unpublished). It is therefore concluded that the stria terminalis is concerned with the affective reactions reported in this paper and that it forms specific connexions between the active areas of the amygdala and hypothalamus.

The results obtained from the amygdala confirm the observations of Kaada *et al.* (1954, 1957) with regard to the basal nucleus, of MacLean & Delgado (1953), Magnus & Lammers (1956), and Kaada & Ursin (1957) with regard to the central and medial nuclei. The responses elicited at the level of the anterior commissure and the preoptic area are in agreement with the findings of Hess & Brügger (1943). The results reported here do not, however, confirm the statement that the lateral nucleus (Kaada *et al.* 1954) and the ventral part of the basal nucleus of the amygdala (Magnus & Lammers, 1956) also form a part of the responsive field, nor do they support Kaada's statement that stimulation of the fimbria fornicis and hippocampus causes bewilderment, fear and anger (see Kaada *et al.* 1953, p. 849, Fig. 3). Discrepancies in results may be due to dissimilarity of electrodes and stimulation parameters used.

Within the amygdala Kaada & Ursin (1957) separated the structures responsible for fear and anger reactions into two zones, the zone concerned with fear reactions lying in lateral portions, the zone concerned with anger reactions lying in mediobasal portions of the amygdala. In the present experiments the points yielding flight, comparable to the 'fear' reaction of Kaada & Ursin, lay scattered between those yielding growling and growling-hissing, comparable to their 'anger' reaction.

Stimulation of the hippocampus (close to the amygdala), the descending column of the fornix, the mammillary bodies and the anterior nuclei of the thalamus—structures constituting the major part of an anatomical circuit connecting the hypothalamus with the cortex (cingulum) and possibly involved, according to Papez (1937), in the elaboration and expression of emotion in man—yielded alertness and uneasy mewing, but never produced elementary affective reactions such as growling, hissing and flight. The present results indicate that the structures that underlie these affective reactions are subcortical and extend, as is shown in Text-fig. 2, from dorsomedial parts of the amygdala by way of the stria terminalis to its bed, becoming continuous with the preoptic area, and still further back, as previous studies have shown, with the intermediate zone of the hypothalamus (Hess & Brügger, 1943; Hunsperger, 1956) and the central gray matter of the mid-brain

(Hunsperger, 1956). It will be observed that all these structures, considered as as entity, lie close to brain cavities—lateral ventricle, infundibulum and Sylvian aqueduct.



Text-fig. 2. Schematic illustration showing the field for affective reactions in forebrain and brain stem based on the active points illustrated in Text-fig. 1 of this paper and in Fig. 1, p. 74, of the report on effects obtained from the brain stem (Hunsperger, 1956).

Two sagittal levels are plotted in one figure.

active field of amygdala, stria terminalis and stria terminalis bed, continuing into

active field of the hypothalamus and the central gray of the mid-brain. Black 'inner zone' yielding hissing; hatched 'outer zone' yielding flight.

A–H planes of frontal sections which are illustrated in Text-fig. 1. For abbreviations see Text-fig. 1.

Comparison of response patterns obtained from forebrain and brain-stem levels

The reactions elicited from this active field, extending from forebrain to brain stem, varied according to the level stimulated. The characteristic affective pattern at forebrain levels was growling, at brain-stem levels hissing and flight. Whereas increased stimulation at the forebrain level finally produced hissing, shrieking or flight, increased stimulation in the brain-stem areas yielded hissing culminating in aimed attack or giving way to flight. Flight, produced as sole response to low-intensity stimulation, was seldom obtained from the forebrain, and when it did occur, appeared to be unpremeditated. In the brain stem, however, flight was regularily produced from the 'outer' zone, i.e. a zone surrounding the 'inner' zone that yielded hissing (Hunsperger, 1956). The animal always sought an outlet before escaping. These results are summarized below together with threshold values.

	Forebrain level (field of the amygdala and the stria terminalis)	Brain-stem level (field in the gray matter of the hypothalamus and mid-brain)
Basic pattern	Growling	Hissing (affective defence reaction, Hess & Brügger, 1943)
Average stimulation threshold (frequency 8·5 c/s, impulse duration 10 msec)	Above 1·5 V	Below 1·5 V
Effect of increasing strength or rate of stimulation	Growling-*hissing* Growling-*shrieking* Growling-hissing-*flight*	Hissing-*attack* Hissing-*flight*
Related pattern	Flight (unpremeditated)	Flight (after seeking an outlet)
Location of points	Scattered between points yielding growling	Zone surrounding the zone yielding hissing

From the experiments reported it is concluded that a substratum, lying in the walls of the ventricles and extending from the forebrain to the brain stem, is concerned with the elaboration of elementary affective reactions. The responses obtained within this substratum are not identical, growling being the characteristic response elicited at forebrain levels, hissing and flight the reactions produced at brain-stem levels.

SUMMARY

1. The amygdala, stria terminalis, and adjacent structures in the forebrain were stimulated in unanaesthetized freely moving cats. The responses were recorded by protocol and film, special attention being paid to the affective reactions evoked. The structures concerned with affective patterns were delimited by mapping the histologically examined positive and negative points.

2. The affective reaction most consistently obtained with low-intensity stimulation was growling integrated in a defence pattern, the latter characterized by lowering of the head, flattening of the ears, dilatation of the pupils, and pilo-erection of back and tail. When stimulation was increased, the growls grew louder, or were followed by hissing, the defence pattern being accentuated by hunching of the back; sometimes the growling was followed by shrieking, or the growling-hissing response led to sudden flight. Flight as a primary response to weak stimulation and hissing as a primary response to stronger stimulation were rarely observed.

3. The area from which these reactions were obtained extends from the

dorsomedial part of the amygdala along the stria terminalis to the stria bed at the level of the anterior commissure, and further back to the preoptic area and rostral hypothalamus; at which level the responsive area joins the active field of the hypothalamus and mesencephalon, previously delimited.

4. The growling response is the characteristic reaction obtained from the amygdala and the stria terminalis, whereas the hissing and flight responses distinguish the effects obtained from the related structures in the hypothalamus and mesencephalon.

5. The active areas in forebrain and brain stem constitute an unbroken subcortical system situated within the walls of the inferior horn of the lateral ventricle, the infundibulum, and the Sylvian aqueduct.

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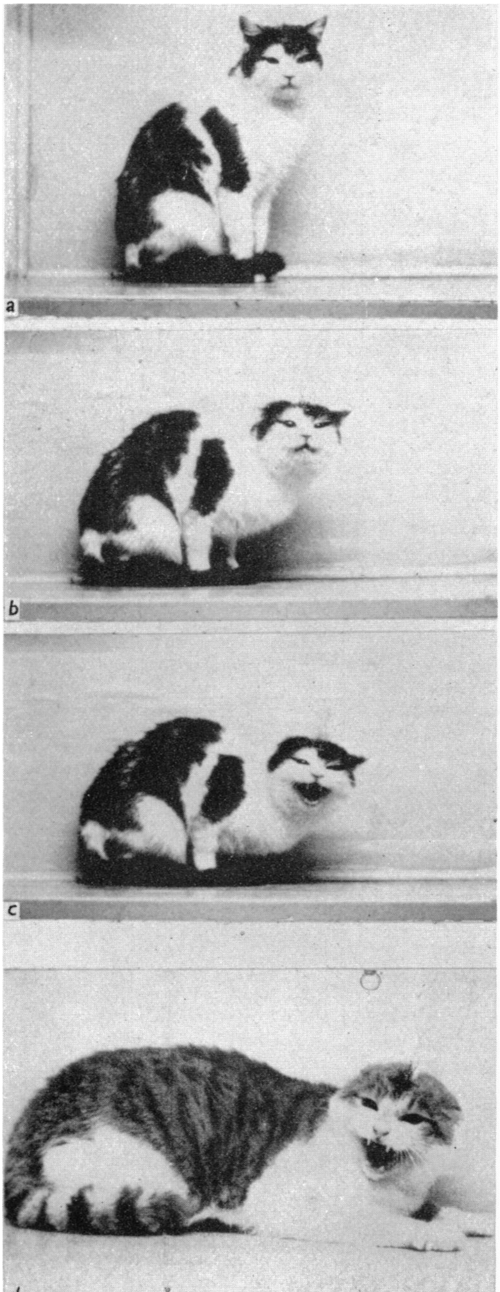

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EXPLANATION OF PLATE

Cats showing reactions described. *a–c*, Growling leading to hissing elicited by electrical stimulation of the dorsomedial part of the amygdala (expt. 116). (*a*) Before onset of stimulation. (*b*) After 25 sec stimulation: growling—note lowering of the head, flattening of the ears, dilatation of the pupils and pilo-erection. (*c*) After 35 sec stimulation: hissing—note accentuated defence pattern. (*d*) Hissing following growling obtained from the stria terminalis bed in another experiment (expt. 139).